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Nesting Behavior of *Podalonia robusta* (Cresson) (Hymenoptera: Sphecidae)

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Abstract .—Twenty-seven females of *Podalonia robusta* were observed nesting in upstate New York during 1980-1985. Females nested solitarily from early June through early October but did not overwinter. They captured cutworms by unearthing them from the soil, stung them several times, cached them, usually on a plant above ground, and dug a burrow some distance away. Prey transport was forward on the ground in a relatively straight line to the nest entrance. Nest closure involved filling the burrow with soil and debris and hammering this fill into place with the head. Nests were unicellular, short, shallow and contained a single prey. Prey consisted of eight genera of hairless, nocturnal-feeding, larval Noctuidae. The wasp's egg was attached to an anterior abdominal segment near the midline. The nesting behavior of *P. robusta* is similar to that of other species in the genus.

The genus *Podalonia* is represented throughout all of the major temperate and tropical regions of the world, except South America (Bohart and Menke 1976). There are 19 species of *Podalonia* in North America north of Mexico (Krombein 1979). O'Brien and Kurczewski (1982) summarized what is known about the biology of the Nearctic and Palearctic species in a paper on the ethology and overwintering of *P. luctuosa* (Smith).

Podalonia robusta (Cresson) is a widely distributed species in North and Central America. It occurs transcontinentally in Canada and the United States as far northward as the North West Territories and the Yukon and as far southward as Costa Rica (Krombein 1979). The species is often confused with *P. violaceipennis* (Lepeletier) because the two are the same size, are black with similar reddish markings and have overlapping geographic distributions, although Murray (1940) gave reliable characters for their separation. In our experience, *P. violaceipennis* tends to be a more coastal species in the northeastern U.S. while *P. robusta* is found more inland, often away from water. The same ecological separation holds true for the two species in Michigan (O'Brien 1989). Our study of the nesting behavior of *P. robusta* was undertaken in order to compare the individual behavioral components of this species with those of other species in the genus, particularly *P. violaceipennis*.

STUDY AREAS

Podalonia robusta was studied at three localities in upstate New York: (1) sandy ridge 2.3 km E Auburn; (2) sandpit 2.0 km S Auburn; and, (3) periphery of active sandpit nr. Junius Ponds, Seneca Falls, all in Cayuga County. Dates of observation are as follows: 27 Aug. 1980, 5 June - 25 Aug. 1981, 30 June - 30 July 1982, 10 Sept. - 3 Oct. 1983, 7 - 23 Sept. 1984, 8 July - 17 Sept. 1985. Voucher specimens of wasps and prey associated with nesting activities are labelled DJP-1, PR81-1-3, PR82-1-6, PR83-1-4, PR84-1-7, PR85-1-6 and have been deposited in the insect museums of Cornell University, The University of Michigan and the S.U.N.Y. College of Environmental Science and Forestry.

FEMALE ACTIVITY

Females of *P. robusta* were observed nesting from 5 June (1981) to 3 October (1983) during partly cloudy to sunny days at ambient temperatures of 18-31C and soil surface temperatures of 37-46C from 1100 to 1735 (EDT). The inclusive dates of collection and observation for this species suggests two generations of wasps per year if the average life span of a female is 6-8 weeks, as in the related genus *Ammophila* (Hager and Kurczewski 1986). Adult overwintering is considered unlikely in this species because 11 wasps marked in the fall were

not recaptured the following spring nor were they seen nesting during warm, sunny days in late April and May. During cool weather, in September and October, all observed nest entrances (N = 13) faced southward.

HUNTING BEHAVIOR AND PREY CAPTURE

In the genus *Podalonia*, the typical nesting sequence is prey capture, cachement, burrow excavation, prey retrieval, provisioning, and nest closure. Females of *P. robusta* were seen on sand near vegetation, running with their faces close to the ground, abdomens pointed upward and tapping their antennae at the bases of plants. One wasp traversed an area 3 m long in 7 min, turning many circles near vegetation. Her unsuccessful search for prey lasted 44+ min, and then she flew away to feed on *Daucus carota*.

Females that searched for prey tapped their antennae on the ground, buzzed their wings audibly and removed soil with their mandibles and forelegs. Such wasps (N = 7) unearthed their prey by digging around the cutworms with the mandibles and forelegs, grasped them with the mandibles and pulled them backwards onto the soil surface. The prey was stung in the ventral side of the body several times, as described for *P. luctuosa* by Steiner (1983). Females then used the mandibles to knead the underside of the anterior segments and midsection of the cutworm's body.

PREY CACHEMENT

Podalonia robusta females (N = 25) cached their immobilized prey on low vegetation, especially grass blades or dried stems, from 2 to 6 cm above ground level. One cutworm was placed in the axil of a goldenrod, 22 cm above the ground. Females (N = 21) began excavating a burrow within 3 m of the cached prey, but four wasps dug as far away as 5.5, 7, 13 and 16 m from their paralyzed cutworm. The nearest to her prey a wasp dug was 12 cm. Prior to digging, females examined the prey thoroughly with their antennae and mouthparts and nine wasps repositioned, restung and/or remalaxated it.

BURROW CONSTRUCTION

Females of *P. robusta* often made several false starts before staying in one place and excavating a burrow. Wasps began burrows by loosening the soil with the mandibles; they then used the forelegs in unison to throw the soil backward beneath the raised abdomen. During burrow excavation the wings buzzed audibly. In addition wasps removed soil backward with the psammophore (see O'Brien and Kurczewski 1982) and placed it a few or several centimeters from the opening. Soil deposited near the entrance was subsequently raked backward with the forelegs, forming a fan- or crescent-shaped low mound. Two wasps dug rapidly in comparison to conspecifics and completed burrows in 11 and 13 min, respectively, at soil surface temperatures of 44-46C. A third female interrupted digging to return to her cached cutworm five times and, upon each return, stung it once in a ventral, anterior segment and then malaxated or fed upon haemolymph exuding from the sting puncture. Following the last sting she rubbed the tip of her abdomen on the sand four times in different areas at distances of 30-150 cm from the quiescent prey. She then cleaned the sting and end of abdomen with the hindlegs, the antennae with the forelegs and resumed burrow excavation. Most wasps groomed themselves upon completion of the burrow.

ORIENTATION

After digging their burrows, females oriented to their nest entrances by walking in circles in either rotation on the ground around them. Some wasps entered and exited from the burrow one or more times while others moved increasingly farther from the entrance, walking in circles. Females then walked or ran toward the cached prey in a rather straight line, sometimes interspersed with short straight flights, but often turned 360° upon landing. Fourteen wasps moved the paralyzed cutworm to a new cache nearer the entrance, returned to the burrow and repeated the orientation behavior described above prior to depositing the prey near the opening. Eleven females proceeded to the nest in a nearly straight line without releasing the prey.

PREY TRANSPORT

Females transported the cutworm, which was often many times heavier than the wasp, to their nests on the ground in an almost straight line. During transport, the prey was held ventral side upward behind the head with the wasp's mandibles and around the thorax with the forelegs. Females, especially those with large cutworms, paused frequently during transport, released the prey and groomed themselves. Some wasps then walked straight forward or in circles, as if attempting to

reorient themselves to their surroundings, before resuming transport to the nest. One wasp released the prey four times and each time stung it in a different abdominal segment, beginning with the second segment and working backward. After her final sting she released the cutworm, reoriented by walking in circles, regrasped the prey and walked straight toward the nest entrance. Another wasp continued to recache the prey above ground, walked to the entrance, reoriented, walked back to the cutworm, resumed transport, recached the prey, etc. A third wasp retrieved her paralyzed cutworm and transported it for 16 m on the ground through a dense field in a straight line from the cachement site to the nest entrance. This transport took 13 min, following a 42 min interlude of digging, orientation, reexamination of the prey, etc.

At the nest entrance the cutworm was released with its head toward the opening. The wasp entered the burrow, turned around inside, emerged headfirst, and pulled in the prey headfirst with the mandibles.

One wasp, after taking an exceptionally long (38 mm) cutworm inside, pulled it backwards out of the nest, reentered and began enlarging the burrow. She then emerged headfirst and pulled in the prey.

NEST CLOSURE

After ovipositing on the cutworm, females appeared headfirst in their entrances ca. 1 min after entry, began breaking off pieces of the entrance with the mandibles and placed these inside the burrow. Wasps then either threw soil backward into the opening with the forelegs or retrieved clumps of soil from the surface with the mandibles and placed these inside. This soil was packed into the opening with the head. Some wasps then brought pebbles, seeds, dried leaves, twigs, and/or agglutinated sand clumps from a bee tumulus and incorporated these into the fill. A few females continued to place pebbles up to 9 mm in diameter, twigs, seeds and other debris atop the filled entrance. Alternately, they threw loosened sand onto the fill and surrounding area with the forelegs which totally concealed the entrance. Nevertheless, a few filled nests remained depressed 2 mm at the entrance. Upon completion, wasps hovered in flight for a second or two and then flew away. One closure, completed at 1432 took 11 min. Excavation of another nest revealed that a female had stayed inside of her cell, head outward, atop the cutworm for 21 min without ovipositing, possibly in response to a cleptoparasitic fly attack.

NEST

Nests of *P. robusta* were simple unicellular burrows which sloped downward and were either straight, C- or L-shaped. The circular entrances were 5-9 (mean = 6.9, N = 16) mm and the burrows 5-9 (mean = 6.8, N = 20) mm in diameter. The burrows had a mean length of 24.5 (range = 10-38, N = 25) mm and a mean cell depth of 20.7 (range = 10-38, N = 25) mm. Cells ranged in length from 15-25 (mean = 19.4, N = 25) mm and in width from 7.5-17 (mean = 10.7, N = 25) mm. Tumuli associated with some of these nests measured 35-45 (mean = 40.1, N = 7) mm long, 25-45 (mean = 36.0, N = 7) mm wide and 13 mm (N = 1) high. Differences in nest dimensions between spring and midsummer nesting aggregations of wasps were insignificant (t test, $P > 0.05$).

PREY

Podalonia robusta females preyed upon soil-dwelling, larval Noctuidae. A single paralyzed cutworm was placed in each cell. Prey were determined as follows: *Aletia oxygale* (Grote) (1), *Apamea* sp. (2), *Caenurgina erechtea* Grote (1), *Eupsilia devia* (Grote) (2), *Euxoa* sp. (2), *Lacanobia subjuncta* (Grote & Robinson) (2), *Protorthodes oviduca* (Guenée) (3), ? *Protorthodes* sp. (1) and *Pseudorthodes vecors* (Guenée) (1). Cutworm prey ranged in wet weight from 166 to 698 (mean = 330.1, N = 24) mg and the female wasps weighed 56-83 (mean = 73.8, N = 6) mg. The mean weight of prey to wasp ratio was 4.5: 1.

EGG

Each egg of *P. robusta* was attached by its anterior end to the abdominal midline of the prey; the posterior end of the egg extended away from the midline of the prey's body (N = 17). Live eggs ranged from 3.0 to 4.0 (mean = 3.6, N = 3) mm long and from 0.8 to 0.9 (mean = 0.9, N = 3) mm wide. They were placed on the left (6) or right (11) sides of the cutworm and were affixed to the first (1), second (2), third (5), fourth (8) or fifth (1) abdominal segments.

CLEPTOPARASITISM

Females of *P. robusta* were trailed and their prey or entrances larviposited on/within by three species of Miltogrammini: *Senotainia trilineata* (Van der Wulp), *S. vigilans* Allen and *Sphenometopa tergata* Meigen (Spofford and Kurczewski 1990). One cutworm attacked during prey transport contained 12

maggots of *S. vigilans*. Two wasps attracted three *S. vigilans* while fighting with each other. The first female went off hunting trailed by one fly and the second left hunting trailed by the two other flies. Another *S. vigilans* followed a wasp during prey transport and attempted twice to larviposit on the cutworm. After the *P. robusta* cached her prey, the fly perched motionless on a plant nearby. As the wasp walked away, searching for a place to dig a burrow, the fly followed her and ignored the cached cutworm. One wasp, whose prey was larviposited upon by an *S. trilineata* during transport, did not exit from her nest after placing the cutworm inside. During excavation of the nest, several minutes later, she was observed resting atop the prey which was in a curled, C-position in the cell. There was no wasp's egg on the cutworm. We believe that the wasp was in the process of cleaning maggots from the prey when we unearthed her, but prey cleaning has not been substantiated for species in this genus.

DISCUSSION

In many genera of Sphecidae, certain behavioral characteristics apply to all or most congeners, and species of *Podalonia* are no exception. Key differences exist between species of *Podalonia* as to: (1) whether adult females overwinter; (2) whether the wasps construct burrows before or after capturing prey; and, (3) kinds of prey. Murray (1940), based upon Newcomer's (1930) and Hicks' (1931) observations and his own collecting records, concluded that some adult females of *P. communis* and *P. luctuosa* overwinter. Females of several European species of *Podalonia* are also believed to overwinter (Roth 1928, Maneval 1939, Grandi 1961). O'Brien and Kurczewski (1982) marked *P. luctuosa* females with paint in late summer and recaptured some of them the following spring to confirm overwintering in this species. According to the present study, adult females of *P. robusta* do not overwinter.

At least two species of Nearctic *Podalonia*, *valida* (Steiner 1975) and, sometimes, *occidentalis* (Evans 1987) dig their burrows before they hunt for prey. This behavior has also been reported in two exotic species of the genus (Tsuneki 1968, Bohart and Menke 1976). The advantages and disadvantages of digging the burrow before prey capture have been reviewed by Evans and West-Eberhard (1970) and Iwata (1976). *P. robusta* invariably dug its burrow after capturing prey, in our observations of 27 wasps.

The majority of species of *Podalonia* prey upon hairless, nocturnal-feeding, noctuid larvae (Bohart and Menke 1976, Krombein 1979). *P. valida*, in contrast, hunts diurnal "wooly bears" of the genus *Estigmene* (Arctiidae) (Steiner 1974), and *P. occidentalis* is a specialist on tent caterpillars of the genus *Malacosoma* (Lasiocampidae) (Evans 1987). Williams (1928) noted that *P. violaceipennis* also captured tent caterpillars in California, but it is likely that he, too, was observing *P. occidentalis* (Evans 1987). Balduf (1936) reported that *P. violaceipennis* hunts mature larvae of the notodontid *Symmerista albifrons* S. & A., but his report may have involved misidentification of the wasp. Roth (1928) observed *P. hirsuta* Scopoli preying upon gypsy moth larvae (Lymantriidae) in Europe. That three species of *Podalonia* capture hairy, arboreal, lepidopterous larvae and numerous other species prey upon hairless, nocturnal-feeding cutworms is a difference that provides the basis for further study of prey selection in the genus.

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